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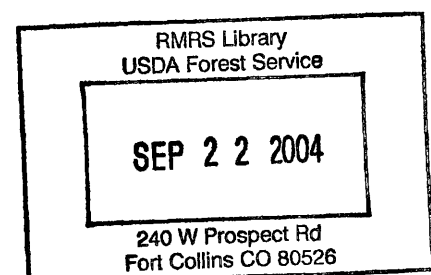
DO PARASITIC PLANTS RECRUIT PREDATORS BY CHANGING HOST  
MORPHOLOGY?

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## ABSTRACT

We investigate the hypothesis that parasitic plants protect themselves from herbivores by altering host-plant morphology to increase predation and thereby reduce herbivory. Published studies provide support for the notion that plants influence predator–herbivore interactions, and thus plants are subject to selection from a third trophic level. Examples from numerous taxa illustrate that many parasitic plants profoundly affect host-plant morphology. These generalities individually support the hypothesis, but they do not connect its four links—parasite, host, predator, and herbivore.

We experimentally tested the hypothesis in two field studies. First, we investigated whether the parasitic plant, southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*) increases local predator abundance by altering the branch morphology of Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum*). Branches infected by this mistletoe displayed a reticulate morphology collecting 35 times more dead needles and supporting 1.8 times more predatory arthropods than similar-sized, but non-infected branches. Second, we investigated whether arthropod predators prey upon lepidopteran herbivores of dwarf mistletoe and reduce herbivory of the parasite. Over a 30-day trial, herbivores fed upon approximately two-thirds of available mistletoe shoots. Removal of arthropod predators increased herbivore survival by 56 percent, but removal in this case did not significantly reduce herbivory.

We speculate that herbivores were sufficiently abundant in our test that they competed for access to mistletoe shoots and surviving herbivores compensated for predation losses with greater per capita feeding. Our empirical investigations confirm each of the four, individual, direct interactions required to support our hypothesis (parasite → host morphology → predator abundance → herbivore abundance → parasite damage). We advocate additional study to test a chain of indirect interactions, whereby parasites increase their fitness through a cascade of effects beginning with change to host phenotype.

KEYWORDS: tri-trophic, plant defense, host–parasite interaction

## INTRODUCTION

There is a growing understanding that plant phenotype can influence rates of predation on its herbivores and that plants may therefore be under selection from a third trophic level (Price et al. 1980, Marquis and Whelan 1996). We add the observation that parasitic plants control not only their own but also their host's phenotype (Kuijt 1969, Hawksworth et al. 1996). Combining these two ideas, we review the evidence that parasitic plants increase their fitness by facilitating predator consumption of herbivores through manipulation of host plant phenotypes. Then, we identify the criteria required to characterize the likelihood of such a scenario. Finally, we present the results of two experiments investigating whether parasitic southwestern dwarf mistletoe (*Arceuthobium vaginatum* (Willd.) Presl subsp. *cryptopodum* (Engelm.) Hawksw. & Wiens) reduces damage from lepidopteran herbivores through morphological changes to its host, Rocky Mountain ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. & C. Laws. var. *scopulorum* Engelm.).

### Evidence of selection from the third trophic level

Herbivores present one of the greatest biotic challenges to plants (Howe and Westley 1988, Abrahamson 1989, Price 1991, Olff et al. 1999, Herrera and Pellmyr 2002). The means by which plants resist, tolerate, or avoid damage by herbivores has long been a topic of great interest in ecology and evolutionary biology (Feeny 1976, Rhoades and Cates 1976, Coley et al. 1985, Herms and Mattson 1992). Not only do plants maintain multiple in situ mechanical and chemical defenses against herbivores, they also appear to benefit from ex situ biotic defenses, whereby predators protect plants from herbivores (Janzen 1966, Price et al. 1980). Removing biotic defenses (i.e., predator exclusion) can result in the increase of herbivore damage to plants (Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001, Shurin et al. 2002). Given the potential benefits to plants from predator control of their herbivores, plant characters may be selected that facilitate predator effectiveness. Plants influence predator-herbivore interactions in at least four ways. Plants can 1) attract predators or delay their departure, 2) increase the time herbivores are exposed to predators, 3) reduce or eliminate enemy-free space, and 4) increase the likelihood of herbivore discovery by predators.

Plants attract and retain predators through special structures, chemicals, and morphology. Some plants produce extra-floral nectaries and Beltian bodies for feeding and domatia for housing predatory mites and ants (Odowd et al. 1991, Odowd and Willson 1991, Walter 1996, Agrawal and Karban 1997, Norton et al. 2001; Janzen 1966, Huxley and Cutler 1991). Plants attract predators by release of volatile chemicals when damaged by herbivores (Bedard et al. 1980, Dixon and Payne 1980, Turlings et al. 1990). Turlings et al. (2002) presents evidence that production of these secondary compounds is affected by selection. Morphology including branching architecture and surface features reduce the likelihood of predators falling off the plant (Juniper and Southwood 1986, Kareiva and Sahakian 1990).

Plants also affect herbivore-predator interactions through direct plant effects on herbivores. Plants can increase predation on herbivores by sub-lethal defenses that slow herbivore development and thereby prolong exposure to predators (Clancy and Price 1987, Haggstrom and Larsson 1995, Benrey and Denno 1997, Devine et al. 2000, Fordyce and Shapiro 2003; but see

Lill and Marquis 2001). Mechanical defenses slow herbivore movement and feeding, increasing the time spent in microsites accessible to predators (Juniper and Southwood 1986). Induced chemical defenses increase herbivore movement within and among plants, placing them in more locations for discovery by predators (Karban and Baldwin 1997, Agrawal et al. 1999, Tollrian and Harvell 1999). Finally, plant chemistry influences herbivore palatability through insect sequestering of secondary plant compounds (Stamp and Bowers 1996, Theodoratus and Bowers 1999).

Plant morphology increases predator efficacy by reducing enemy-free space (Marquis and Whelan 1996). For example, twig diameter and length, branching angles, and the distance between twigs can affect access by foraging birds and lizards (Whelan 2001, Moermond 1986). The particular architecture of some aquatic macrophytes either exposes or protects snails from fish predators (Covich and Knezevic 1978). Finally, plants can counter the herbivore's attempts to create enemy-free space by galling and leaf-tying (Karban and Agrawal 2002, Crespi et al. 1997, Harris et al. 2003, Ollerstam and Larsson 2003, Stone and Schonrogge 2003, Marquis et al. 2002).

Plants influence predator abundance through morphologies that determine the degree of canopy and surface complexity. Langellotto and Denno (2004) conclude predator abundance is significantly increased (in some cases) with greater habitat complexity. A more complex canopy architecture, however, can reduce herbivore–predator encounters (Holling 1959, Casas and Djémai 2002). For example, habitat complexity increases the effort required for the parasitoid *Trichogramma* to locate host egg masses (Andow and Prokrym 1990, Lukianchuk and Smith 1997, Gingras et al. 2003). Kaiser (1983) reports that predator–prey encounters are more frequent for predatory and prey spider mites on leaves with shorter margin length (entire, rather than lobed or toothed). Whether by morphology or chemistry, heritable plant characteristics appear to affect predator–herbivore interactions to the potential benefit of host fitness.

#### Evidence that parasitic plants use host phenotypes to their advantage

Animal and other parasites frequently change the phenotypes of their hosts in ways thought to be adaptive to the parasite (Barnard and Behnke 1990, Moore and Gotelli 1990, Moore 1995, Moore and Gotelli 1996, Beckage 1997, Moore 2002). Gall-forming insects change plant phenotypes by inducing the production of elaborate domatia that include resources to feed and protect the parasite (Crespi et al. 1997, Stone and Schonrogge 2003). Ewald (1994) reviews evolutionary interactions of various disease-causing agents and their hosts. One might even consider the host plant as an “extended phenotype” of the parasite used to its own reproductive benefit besides the obvious nutritional use (see van Ommeren and Whitham 2002).

Flowering parasitic plants also change host physiology and resulting morphology in fixed and characteristic ways that imply a genetic basis to plant disease (Kuijt 1969, Hawksworth et al. 1996). Although resource redistribution within the host and acquisition by the parasite undoubtedly contribute to the parasitic etiology, altered host phenotypes—disease symptoms—are the result of numerous host–pathogen interactions. For example, Livingston et al. (1984) describe elevated levels of plant growth regulators associated with infection by dwarf mistletoe (*Arceuthobium*, Viscaceae). Dwarf mistletoe, thereby, induces the host to form witches' brooms



on infected branches (Geils and Hawksworth 2002). Brooms (Fig. 1) are a preferred growth sink; they persist when other branches self-prune; and they form numerous but short secondary branches. The formation and type of broom depends on and is consistent with the species of mistletoe and host. These parasitic plants appear to have a variable and inherited capability to affect host phenotype through parasitism of infected branches. Tinnin et al. (1981) speculate how brooms may be adaptive for the mistletoe by retarding replacement of the host species with later successional species.

### Testing for the adaptive value of parasite-induced changes to host morphology

Could parasite-induced changes to host morphology attract predators and thus provide protection to the parasite from its herbivores? For selection to act in this way, a minimum of four criteria must be met (Fig. 2). First, the parasitic plant must alter host morphology; this ability must be variable and heritable. Second, these parasite-induced changes to host morphology must increase either the local abundance of predators, or the per-capita effects of predators on herbivores. Third, these predators must reduce the abundance of parasitic plant herbivores, or the per capita effects of these herbivores on parasitic plant. And fourth, these herbivores must reduce reproductive success of the parasite and therefore, its fitness. Finally, this series of four direct interactions (parasite → host morphology → predator abundance → herbivore abundance → parasite damage) must also produce the implied indirect interactions whereby parasitism increases predation and predation reduces herbivory and herbivory reduces parasite reproduction.

We conducted two experiments that together test four criteria (Fig. 2). In the first experiment, we characterized the ways in which dwarf mistletoe modifies its host-pine morphology (criterion #1); and we documented the indirect effects of these modifications on the pine arthropod community (criterion #2). Identified differences in the arthropod assemblage between parasitized and unparasitized branches would constitute a previously under recognized indirect effect of plant parasites on host arthropod communities. In the second experiment, we identified the effects of the pine arthropod community on mistletoe herbivores (criterion #3); and we examined whether, through a tri-trophic interaction (*sensu* Price et al. 1980), canopy predators would provide a fitness advantage to the parasite by reducing rates of herbivory (criterion #4). Although documenting these four direct criteria do not prove the implied indirect effects (Wootton 1994), a demonstration of these direct interactions would establish the possibility parasitic plants can gain a fitness advantage through manipulation of host morphology.

## METHODS

### Field site, southwestern dwarf mistletoe and associated species

We conducted field work at the Manitou Experimental Forest (39° 06' 30" N, 105° 06' 55" W), Woodland Park, Colorado, U. S. A. We worked in forest stands of ponderosa pine at an elevation of 2400 m. Southwestern dwarf mistletoe is a widespread, abundant, and damaging parasite of Rocky Mountain ponderosa pine in this area.

In common with all dwarf mistletoes, southwestern dwarf mistletoe is a shrubby, aerial parasite of conifers; mistletoe plants are dioecious, with reduced leaves and flowers. Southwestern dwarf

mistletoe plants consist of multiple aerial shoots, 2–5 mm diameter and commonly to 20 cm tall at flowering; shoots emerge through the pine bark from the parasite's endophytic system, embedded in the host's bark and wood. Shoots persist for several years and perform essentially only a reproductive function of supporting the flowers and fruits. The endophytic system is perennial and serves to parasitize the host by extracting water, minerals, and carbohydrates from the host (Hawksworth and Wiens 1996). Ponderosa pine branches infected with dwarf mistletoe typically develop into brooms (Fig. 1, described above).

The canopies of ponderosa pine are home to a diverse arthropod community. At Manitou, we find over 250 species of arthropods on ponderosa pine branches (Mooney, unpublished data). Coleopteran species dominate this diversity (107 species), but the aphids (Aphididae: Homoptera) *Cinara schwarzii* Wislon (1919) and *Essigella fusca* (Gillette & Palmer 1924) are numerically dominant. Lepidopteran larvae and thysanopterans feed on pine tissues (needles and pollen respectively); psocopterans and collembolans are canopy detritivores. Spiders (Araneae) and mirids (Miridae: Hemiptera) are the most diverse and abundant predators. Where aphids are abundant, ladybird beetle adults and larvae (Coccinellidae: Coleoptera), as well as lacewing larvae (Neuroptera) are common. Several ants are also common (*Formica* spp., [Formicidae: Hymenoptera]). Although ants are predators of many herbivores, they are also mutualists with *C. schwarzii*. Very mobile dipterans and hymenopterans are also abundant, but they are not limited to ponderosa pine.

Southwestern dwarf mistletoe supports an endemic herbivore fauna (Stevens and Hawksworth 1970, Hawksworth et al. 1996, Mooney 2001, Mooney 2003). At Manitou, these animals include the herbivorous mirid *Neoborella tumida* Knight 1925 (Hemiptera: Miridae), an unidentified herbivorous mite (*Acari*), and three species of dwarf mistletoe-specialist lepidopteran larvae. These specialist species are the common *Dasypyga alternosquamella* Raganot 1887 (Pyrilidae) and *Promylea lunigerella glendella* Dyar 1906 (Pyrilidae), and the rare *Mitoura spinatorum* Hewitson 1867.

### Experiment 1: Parasitism effects on host morphology and arthropod communities

In this experiment, we characterized differences in morphology and arthropod community for branches parasitized (broomed) or not parasitized (uninfected) by southwestern dwarf mistletoe (Fig.1). In July 2000, we selected 10 parasitized and 10 unparasitized branches from a 2-ha stand of 50 to 60 year-old ponderosa pine trees; all branches were 1 to 2 m above the ground, 1.5 to 3.0 m long, and from a different tree. Typical of ponderosa pine, the pattern of unparasitized branches was dendritic, that is with secondary branches (branchlets) fanning out and not overlapping or crossing. Over time, as a consequence of continued infection, parasitized branches lose their dendritic form and become a dense cluster of crossing branchlets, some pressing on other branchlets. For this experiment, we only selected infected branches as parasitized that had at least three branchlets crossing and touching other branchlets. We selected only branches not apparently infected by mistletoe as unparasitized.

We measured a series of morphological variables on each selected branch. Branch length was determined as the distance along an axis from the tree trunk to the farthest branch tip. The distance between two lines parallel to the length axis, touching the left and right flanks of the

branch defined branch width; likewise the distance between the highest and lowest tips defined branch height. Other metrics were number of branch crosses, branch diameter at base, branch age (from count of annual rings), and the fresh masses of foliated branch tips, remaining bare wood, and accumulated detritus. For analysis, we used MANOVA with branch type (parasitized, unparasitized) as a discrete variable and examined the ANOVA for each dependent variable (excluding the selection criteria, number of crosses). We performed a principle components analysis to reduce potentially correlated variables for branch size to a single variable (PC1, see results) which was used as a covariate in comparisons of arthropod abundance by branch type.

The arthropods found on parasitized branches include both those associated strictly with the pine host and those strictly associated with the mistletoe (Stevens and Hawksworth 1970, Hawksworth et al. 1996, Mooney 2001, Mooney 2003); arthropods found on unparasitized branches are just those associated with ponderosa pine. To isolate the effects of mistletoe parasitism attributable only to changes in host morphology, we removed from our samples the mistletoe plants and their strictly associated arthropods. To collect the remaining, pine-associated arthropods, we beat each branch with a padded stick, thereby dislodging arthropods onto a 2 x 2 m framed sheet. We retrieved each arthropod with a mouth aspirator and deposited it in 70 percent ethanol. We repeated the collection process (usually 3 or 4 cycles), until beating failed to dislodge more arthropods.

We identified the arthropods to order or family and measured their length to the nearest millimeter. For analysis, we grouped taxa and functional groups into eight guilds (to avoid a large number of branches with zero abundance for some categories). The three plant-feeding groups were (1) Sucking herbivores (*C. schwartzii*, *E. fusca*, other aphids [Aphididae, Homoptera] and non-aphid Homoptera [Membracidae, Cicadellidae]); (2) chewing herbivores (Lepidoptera larvae and Thysanoptera); and (3) detritivores (Psocoptera and Collembola). The five predators groups were (1) mites (Acari); (2) spiders (Araneae); (3) Hemiptera (principally predatory genera of *Miridae*); (4) aphid predators (lacewing larvae [Neuroptera], and larval and adult ladybird beetles [Coccinellidae: Coleoptera]); and (5) other predators (ants [*Formica*, Formicidae: Hymenoptera] and pseudoscorpions [Pseudoscorpiones]). To test for an effect of branch type on arthropod group abundance, we performed MANCOVA with arthropod groups as multiple dependent variables, branch type as a discrete predictor, and branch size as a continuous covariate. We followed this with individual ANCOVAs by arthropod group with branch type as a discrete predictor and branch size as a continuous covariate. To test for an effect of branch type on arthropod size distribution, we regressed log(arthropod abundance) and arthropod size (mm size classes). The slope of log(abundance) over size provided single parameters for size distribution by branch type (Dial and Roughgarden 1995). We compared size distributions by branch type (slopes) with ANCOVAs for predators, herbivores, and all arthropods combined.

We conducted all analyses with the SAS statistical package (SAS Institute 2001). We used PROC GLM for ANOVA and MANOVA tests; we used PROC PRINCOMP for principal components analysis. Where multivariate tests were significant, we inspected the results of separate univariate tests without adjusting  $\alpha$  for multiple comparisons per the protocol described by Johnson and Wichern (1998). We adjusted  $\alpha$  using the Bonferroni approach (Zar 1999) for separate univariate tests following insignificant multivariate tests.



### Experiment 2: Effects of predators on southwestern dwarf mistletoe and its herbivores

In this experiment, we examined (1) whether predatory arthropods from the pine branch community prey upon lepidopteran herbivores of mistletoe and (2) whether these predators indirectly benefit mistletoe by reducing herbivory. *Dasypyga alternosquamella* and *Promylea lunigerella* were the dominate lepidopteran larvae. *Promylea* and *Dasypyga* are closely related, and probably sister genera, very similar in size and ecology (Heinrich 1956; Mooney 2001, Mooney 2003). They feed on the surface of, and tunnel within, mistletoe shoots. Feeding often begins at the shoot base, and even a little feeding kills all distal tissue. Prior to this experiment, the combined abundance of these species was 284 larvae on 112 mistletoe plants or 2.5 larvae per plant (Mooney 2001).

On 13 August 1999, we selected 20 ponderosa pine branches (only one branch per tree) infected by at least four mistletoe plants per branch. We chose branches (experimental units) similar in sized and shape. If a branch had more than four mistletoe plants, we completely removed the aerial shoots of all but four plants. We counted the number of shoots of each plant and summed these four sub-totals for a total number of shoots per branch. We then scoured the foliage and bark of ten of these branches with brushes to dislodge all arthropods. On all 20 branches, we visually inspected the mistletoe plants and removed all larvae. We enclosed all 20 branches within large Reemay bags and sealed each bag against the base of the branch with wire.

[footnote: Reemay is a thin, spun-polyester fabric that is both highly breathable and transparent.]

Between 8 and 15 August 1999, we collected mistletoe plants and isolated in excess of 240 third- and fourth-instar larvae of *D. alternosquamella* and *P. lunigerella*. We kept these larvae in individual petri dishes with fresh mistletoe. On 15 August, we placed the dishes in a +5° C refrigerator for 3 hours, transported them to the field site in an insulated cooler, and placed 12 larvae on the mistletoe plants in each bagged, experimental branch (a stocking rate of 3 larvae per plant). On 15 September, we cut the branches, brought them to the laboratory, and froze them for several days to kill all arthropods. We then recorded the number of *D. alternosquamella* and *P. lunigerella* larvae and pupae per branch (survival), identified and counted other arthropods by taxonomic order. We determined the number of mistletoe shoots killed per branch (herbivory).

This experiment offered the following predictions (1) arthropod removal would (a) reduce arthropod abundance or (b) not affect it (never increase it); (2) predator removal would (a) increase lepidopteran abundance or (b) not affect it; (3) predator removal would increase (a) mistletoe herbivory or (b) not affect herbivory. Therefore, we conducted all analyses with PROC GLM (SAS Institute 2001) using one-tailed probability tests (Zar 1999).

## RESULTS

### Experiment 1: Parasitism effects on host morphology and arthropod communities

Branches of ponderosa pine broomed (parasitized) by southwestern dwarf mistletoe displayed a different morphology than uninfected (unparasitized) branches (Table 1). The multivariate comparison (MANOVA) for parasitized and unparasitized branches included variables for length, width, height, diameter, age, wood mass, foliage mass, and dead needle mass; the

difference was significant (Wilk's Lambda = 0.1694,  $F(8,11)=6.74$ ,  $P=0.0025$ ). Parasitized branches had significantly (ANOVA) more wood mass and dead needle mass and were on average shorter and older ( $0.10 > P > 0.05$ ). The principal components analysis (Fig. 3) constructed two axes which we interpret as representing branch size (PC1) and parasitized morphology (PC2). PC1 scores for parasitized and unparasitized branches did not differ significantly ( $F_{1,18}=0.08$ ,  $P=0.7792$ ) and were positively and significantly ( $P<0.05$ ) correlated with branch length ( $r=0.29$ ), width ( $r=0.57$ ), height ( $r=0.35$ ), wood mass ( $r=0.90$ ) and foliage mass ( $r=0.65$ ). PC2 scores differed significantly by branch type ( $F_{1,18}=6.38$ ,  $P=0.0211$ ), and were positively and significantly correlated with branch age ( $r=0.28$ ), diameter ( $r=0.60$ ), wood mass (0.43), and number of crosses ( $r=0.53$ ).

Predator community abundance differed for pine branches parasitized or not by dwarf mistletoe (Table 2). The multivariate comparison (MANOVA) by branch type considered abundance of Acari, Araneae, Hemiptera, aphid predators, and other predators; the difference (adjusted for branch size) was significant (Wilk's Lambda=0.37,  $F_{5,12}=4.16$ ,  $P=0.0200$ ). Parasitized branches had significantly (ANCOVA) more mites, more hemipterans, and more of all predators combined.

Herbivore community abundance did not differ for branches parasitized or not by mistletoe (Table 3). The multivariate comparison (MANOVA) by branch type considered abundance of sucking herbivores, chewing herbivores, and detritivores; the difference (adjusted for branch size) was not significant (Wilk's Lambda=0.27,  $F_{7,10}=1.15$ ,  $P=0.4042$ ). Parasitized branches did not have a significantly (ANCOVA) different abundance for any group or for all plant feeders combined compared to unparasitized branches.

Neither the predator community, the herbivore community, nor the combined arthropod community differed in size distribution by branches parasitized or not by mistletoe (Table 4). Arthropods ranged in size from 1 to 14 mm; abundance decreased with increased size (Fig. 4). Regressions of log(abundance) on size were significant for predators, herbivores, and all arthropods; therefore, the slope of log(abundance) on size for each of these groups described size-class distributions (Table 4). No significant effects of branch type interaction with arthropod size were observed for any of the groups; therefore, we failed to detect a influence of mistletoe brooming on size-distribution for the several arthropod communities.

#### Experiment 2: Effects of predators on southwestern dwarf mistletoe and its herbivores

Predator removal was successful at the end of the trial in reducing the number of predators and increasing the survival of herbivores, but the effect of removal on herbivory was unresolved (Fig 5). After 30 days, we found a mean of 4.4 (SE=2.3) predators per branch for those branches we had previously scoured and a mean of 18.7 (SE=3.6) predators per branch for the other sample branches; these differences were significant ( $F_{1,18}=9.31$ ,  $P=0.0034$ ). We also found a mean of 8.6 (SE=1.5) larvae of *D. alternosquamella* and *P. lunigerella* per branch (72% survival) for scoured branches and a mean of 5.5 (SE=1.0) larvae per branch (46% survival) for the other sample branches; these differences were significant ( $F_{1,18}=3.03$ ,  $P=0.0494$ ). There was, however, no significant difference ( $F_{1,18}=0.68$ ,  $P=0.21$ ) in the number of mistletoe shoots per branch for the two treatments. For the scoured branches with fewer predators and more herbivores, we observed

23.1 (SE=3.2) killed shoots per branch (57% of original shoots were damaged). For the other sample branches, however, with more predators and fewer herbivores, more shoots per branch were killed—27.0 (SE=3.4); and a higher percentage were consumed—67%. Finally, the regression of herbivory (fraction of shoots killed) on herbivore survival (fraction of stocked larvae surviving) was not significant ( $F_{1,18}=2.01$ ,  $P=0.17$ ).

We investigated the possibility that failure to detect differences in herbivory (shoot loss) between treatments was due type-II error (i.e., a difference existed, but was not detected; Zar 1999). The 56% increase in larval abundance with predator removal provides a null hypothesis of a similar increase in mistletoe shoot loss in that treatment. We performed a power analysis to determine the probability of detecting a 56% difference in shoot loss ( $d=14$  shoots), given the variance in shoot loss observed ( $s=13.3$  shoots), the sample sizes used in this experiment ( $N=10$  per level of treatment), and a 5% chance of type-I error ( $\alpha=0.05$ ). Based on these values, there was more than an 80% probability that such a difference would have been detected with this current experimental design ( $f>0.80$ ).

[It is unclear to me where you got 56% increase in larval abundance or 56% difference in shoot loss.]

## DISCUSSION

Parasitism by dwarf mistletoe changed host branch morphology and altered the arthropod community. Brooding increased the mass of bare wood by 1.5 times, transformed the branch pattern to reticulate with numerous crossed branchlets; parasitized branches collected 35 times the mass of dead needles. Coincident with these morphological changes was an increase 5.8-fold for mites, 2.9-fold for hemipterans, and 1.8-fold for all predators. [note I came up with different numbers for hemipterians and all predators] Our results were consistent with conclusions by Langellotto and Denno (2004) that increasing habitat complexity with detritus generally increases the abundance of hemipterans and mites. A difference, however, was that they noted an increase in spider abundance that we could not corroborate. There are several mechanisms by which observed changes in branch morphology could increase predator abundance (see Langellotto and Denno 2004). First, the reticulate branch pattern and accumulation of dead needles could create a microclimatic favorable for these arthropods. Second, increased physical complexity could reduce intraguild predation by decreasing encounters among arthropod predators or protecting them from insectivorous birds. Third, the substantial resources of decaying needles could increase detritivore abundance, supporting more predators. Regardless of the specific mechanisms, our experiment supported the first two direct interactions of interest (parasite → host morphology → predator abundance).

During our 30-day experiment, specialist lepidopteran herbivores consumed or killed nearly two-thirds of the mistletoe shoots. Because mistletoe shoots are essential reproductive structures, such herbivory could substantially reduce mistletoe fitness. Predators significantly reduced herbivore survival from 72% to 46%, in support of the third direct interaction of interest (predator abundance → herbivore abundance). The connection, however, between herbivore abundance and level of herbivory (consumption of mistletoe shoots) was less clear and could be due to increased per capita feeding (compensatory) by the fewer, surviving larvae. Although our

stocking rate in 1999 of 3 larvae per mistletoe plant approximated the density determined that year (2.5 per plant), observations in the three following years suggest that herbivores were unusually abundant in 1999. Perhaps, if we had stocked fewer larvae per branch as may be more typical, we would have observed together the third and fourth direct interactions (predator abundance → herbivore abundance → parasite damage). If our experiment had demonstrated that reduced predator abundance resulted in greater herbivory, there would be support for the indirect effect of predators on mistletoe fitness. Nonetheless, this and the previous experiment support by a series of direct interactions the hypothesis—to its benefit, a dwarf mistletoe could alter host morphology, recruit more predators, reduce herbivore abundance, and increase success of flowering shoots.

## CONCLUSION

Our overview of the tri-trophic literature provides strong support for the idea that plants can influence predator-herbivore interactions. If this were the case, then it is also reasonable to ask whether parasitic plants can use host phenotypes in a similar fashion? In our empirical investigation of this hypothesis, we document each of the direct effects required for parasitic plants to increase their own fitness through manipulation of host plant morphology (Fig. 2). These effects are for the parasite to change host morphology, these changes in morphology to increase predator abundance, these predators to reduce parasite herbivores, and the herbivores to consume a large portion of parasite shoots. We also test for some, but not all of the indirect effects that must operate for this scenario to function. We find that parasites indirectly increase predator abundance through host morphology, but we did not demonstrate that predators reduce herbivory by reducing herbivore abundance. Future work should investigate parasite fitness and the rates of predation and herbivory for dwarf mistletoes on pines with various degrees of parasite-induced change in morphology.

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Table 1. Morphological differences between ponderosa pine branches broomed by southwestern dwarf mistletoe (parasitized) or not infected (unparasitized).

Variable	Branch type		df	ANOVA tests		
	unparasitized, mean (1SE)	parasitized, mean (1SE)		ms	F	P
Length (m)	1.9 (0.1)	1.7 (0.1)	1,18	0.01	3.63	0.0728
Width (m)	1.8 (0.2)	1.5 (0.1)	1,18	0.37	2.07	0.1678
Height (m)	1.1 (0.1)	1.1 (0.1)	1,18	0.02	0.22	0.6427
Diameter (mm)	54.0 (2.1)	59.0 (2.8)	1,18	124.70	2.02	0.1726
<b>Wood (g)</b>	<b>2677.5 (442)</b>	<b>4042.5 (370)</b>	<b>1,18</b>	<b>812.51</b>	<b>6.14</b>	<b>0.0234</b>
Foliage (g)	2515.3 (544)	1885 (210)	1,18	0.00	0.1	0.7532
Age (yrs)	26 (3.7)	34.5 (2.8)	1,18	361.25	3.35	0.0838
<b>Dead needles (g)</b>	<b>4.6 (4.6)</b>	<b>164.04 (43.5)</b>	<b>1,18</b>	<b>606.65</b>	<b>34.72</b>	<b>0.0001</b>
Branch crosses*	6.3 (0.8)	0.0 (0.0)				

MANOVA for all variables show significant difference between parasitized and unparasitized branches. Significant univariate tests are highlighted in bold.

\*Number of crosses is used as a selection criterion for parasitized branches and is not included in statistical analyses.

[Did the unparasitized branches have 6.3 crosses or is this a mixup? Even if you used crosses to select parasitized branches, it would be interesting to know how many crosses there were.]

Table 2. Abundance differences for arthropod predator communities between ponderosa pine branches broomed by southwestern dwarf mistletoe (parasitized) or not infected (unparasitized).

	Branch type		ANCOVA tests				
	unparasitized, mean abundance (1SE)	parasitized, mean abundance (1SE)	effect	df	ms	F	P
Arthropods							
<b>Acari</b>	<b>1.4 (0.5)</b>	<b>8.1 (2)</b>	<b>branch</b>	<b>1,16</b>	<b>16.3</b>	<b>17.5</b>	<b>&lt;0.001</b>
			pc1	1,16	1.21	1.3	0.27
			b*pc1	1,16	0.53	0.57	0.46
Araneae	23.2 (5.4)	26.3 (3.8)	branch	1,16	106.0	1.57	0.23
			pc1	1,16	1924.1	28.51	<0.001
			b*pc1	1,16	12.6	0.19	0.67
<b>Hemiptera</b>	<b>10.6 (2.2)</b>	<b>30.8 (5.8)</b>	<b>branch</b>	<b>1,16</b>	<b>2112.4</b>	<b>10.1</b>	<b>0.006</b>
			pc1	1,16	144.5	0.69	0.42
			b*pc1	1,16	13.0	0.06	0.81
Aphid predators	5.4 (1.3)	6.8 (1.6)	branch	1,16	13.0	0.64	0.44
			pc1	1,16	39.3	1.93	0.18
			b*pc1	1,16	25.8	1.27	0.28
Other predators	1.8 (0.6)	2 (0.6)	branch	1,16	0.04	0.04	0.84
			pc1	1,16	0.44	0.54	0.47
			b*pc1	1,16	0.00	0	0.98
<b>All predators</b>	<b>42.4 (7.5)</b>	<b>74 (10.5)</b>	<b>branch</b>	<b>1,16</b>	<b>5733.5</b>	<b>9.56</b>	<b>0.007</b>
			pc1	1,16	4671.2	7.79	0.013
			b*pc1	1,16	94.4	0.16	0.70

MANOVA for arthropod groups show significant difference between parasitized and unparasitized branches. Significant univariate tests are highlighted in bold. ANCOVA effects are for branch type, PC1 score (branch size), and branch type-size interaction.



Table 3. Abundance differences for arthropod herbivore communities between ponderosa pine branches broomed by southwestern dwarf mistletoe (parasitized) or not infected (unparasitized)

	Branch type		ANCOVA tests				
	unparasitized, mean abundance (1SE)	parasitized, mean abundance (1SE)	effect	df	ms	F	P
Sucking herbivores	103.7 (25.8)	54.5 (10.3)	branch	1,16	0.01	1.06	0.32
			pc1	1,16	0.00	0.33	0.57
			b*pc1	1,16	0.00	0.67	0.43
Chewing herbivores	6.1 (1.7)	6.7 (1.9)	branch	1,16	0.00	0	0.97
			pc1	1,16	0.03	0.32	0.58
			b*pc1	1,16	0.00	0.01	0.92
Detritivores	22.8 (5.3)	39.2 (9.5)	branch	1,16	8.92	1.98	0.18
			pc1	1,16	8.80	1.96	0.18
			b*pc1	1,16	6.72	1.5	0.24
All plant feeders	132.6 (24.3)	100 (15.6)	branch	1,16	4427	1.01	0.33
			pc1	1,16	4642	1.05	0.32
			b*pc1	1,16	1526	0.35	0.56

MANOVA for arthropod groups show no significant difference between parasitized and unparasitized branches. No univariate tests are significant. ANCOVA effects are for branch type, PC1 score (branch size), and branch type–size interaction.

Table 4. Size-distribution comparisons for arthropod communities of ponderosa pine branches broomed by southwestern dwarf mistletoe (parasitized) or not infected (unparasitized)

Arthropods	Branch type		ANCOVA tests				
	unparasitized, R <sup>2</sup> , slope	parasitized, R <sup>2</sup> , slope	effect	df	ms	F	P
Predators	0.82, -0.09	0.89, -0.11	branch type	1,24	0.12	3.63	0.0688
			arthropod size	1,24	4.83	147.82	<0.0001
			type*size	1,24	0.05	1.48	0.24
Herbivores	0.69, -0.11	0.68, -0.10	branch type	1,24	0.02	0.20	0.66
			arthropod size	1,24	5.47	51.02	<0.0001
			type*size	1,24	0.02	0.23	0.64
All arthropods	0.89, -0.20	0.93, -0.18	branch type	1,24	0.00	0.00	0.98
			arthropod size	1,24	17.19	220.31	<0.0001
			type*size	1,24	0.03	0.39	0.54

ANCOVA effects are for branch type (parasitized or unparasitized), arthropod size (length), and branch type–arthropod size interaction.

## FIGURE LEGENDS

Figure 1. A now-dead broom of ponderosa pine caused by southwestern dwarf mistletoe that illustrates the abnormal persistence and morphology of a mistletoe-infected (parasitized) branch.

Figure 2. Schematic diagram of the four direct interactions that must occur for parasitic plants to increase their own fitness indirectly through direct control of host-plant morphology. The inner circles show the steps examined by the two experiments described in this article.

Figure 3. Principal component scores of 10 parasitized (small filled circles) and unparasitized (small open circles) branches. Parasitized and unparasitized means (+ 1SE) are shown with large circles.

Figure 4. Size distribution for all arthropods combined on parasitized (filled circles) and unparasitized (open circles) branches. Each circle represents the log(mean abundance) of 10 branches for a size class. The slopes of the lines for parasitized (solid) and unparasitized (dashed) branches do not differ significantly. See Table 4 for detailed statistics. Separate distributions for predators and plant feeders are similar in form, and are not shown.

Figure 5. Mean abundance (+ 1SE) of predators (top), Mistletoe lepidopteran herbivore survival (middle), and mistletoe shoots consumed (bottom) for predator removal (white bars) and control (black bars) branches. Significant differences ( $P < 0.05$ ) are indicated by a '\*'. See text for detailed statistical results:

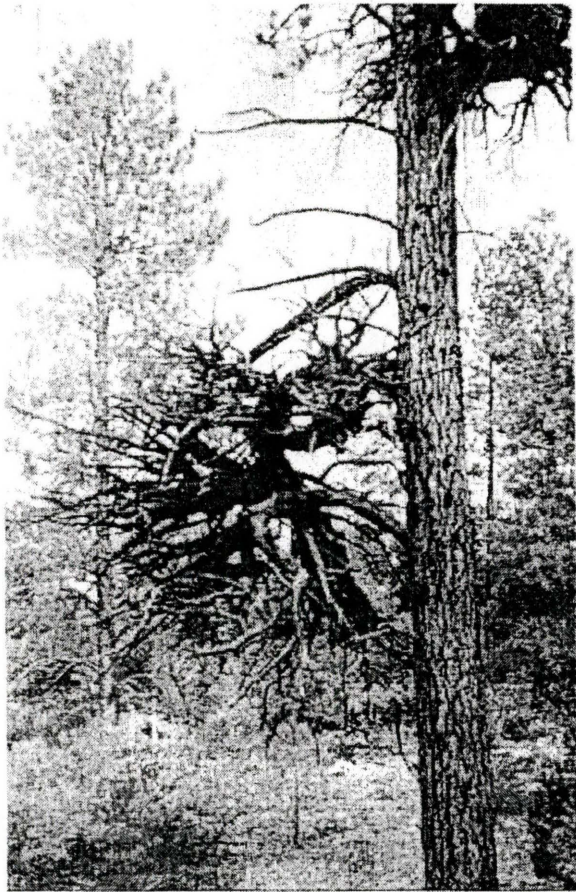


Figure 1

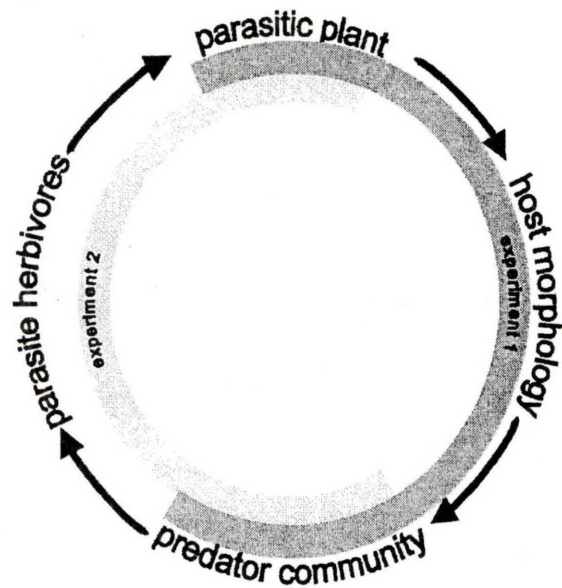


Figure 2

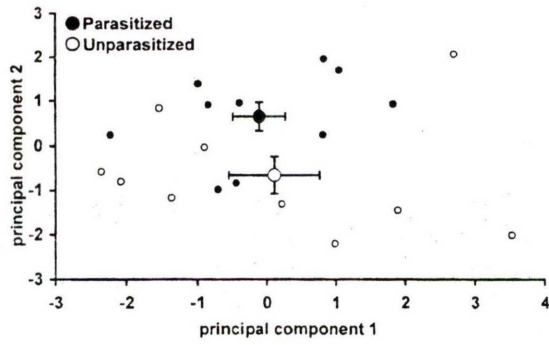


Figure 3

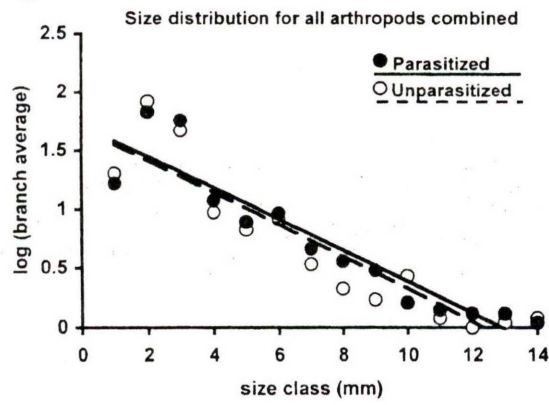


Figure 4

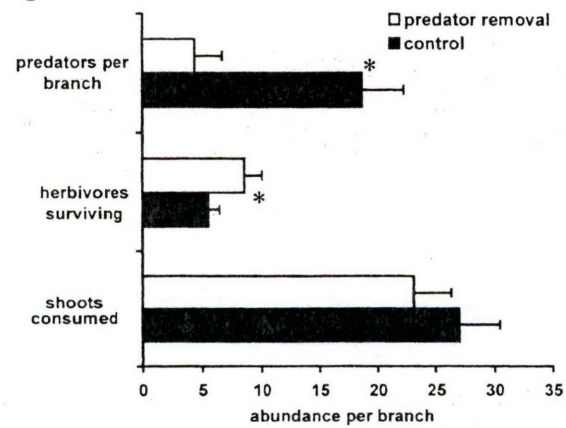


Figure 5



Yan Linhart  
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edu>

To: bgeils@fs.fed.us  
cc:  
Subject: Fwd: RJVA 03-JV-11221606-301

04/28/2004 05:27 PM

Begin forwarded message:

> From: Brian W Geils <bgeils@fs.fed.us>  
> Date: Wed Apr 28, 2004 6:13:03 PM America/Denver  
> To: rmrs agreements <rmrs\_agreements@notes.fs.fed.us>  
> Cc: kailen.mooney@tritrophic.org, yan.linhart@colorado.edu  
> Subject: RJVA 03-JV-11221606-301  
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>  
> I have received and accepted the final report for RJVA  
> 03-JV-11221606-301,  
> University of Colorado, Direct and indirect effects of canopy  
> arthropods on  
> dwarf mistletoe and the conifers they parasitize. The final report is a  
> draft manuscript titled "Do parasitic plants recruit predators by  
> changing  
> host morphology?" by Mooney, Geils, and Linhart (provisionally  
> intended for  
> publication by the peer-reviewed journal Oikos).  
>  
> I have attached below the manuscript, revised by Geils as co-author.  
> The  
> work plan, performance report, and final report have therefore been  
> completed and accepted. I have mailed a printed copy of  
> manuscript/final  
> report and signed the request for reimbursement. Please close this  
> agreement.  
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> (See attached file: manuscript-04-04-28.doc)  
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> =====  
> Mistletoes of North American Conifers, RMRS-GTR-98 is available  
> view at [http://www.fs.fed.us/rm/pubs/rmrs\\_gtr098.html](http://www.fs.fed.us/rm/pubs/rmrs_gtr098.html)  
> request from bgeils@fs.fed.us  
> ~~~~~  
> BRIAN W. GEILS  
> USDA Forest Service, Rocky Mountain Research Station  
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> ~~~~~  
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>  
> Mistletoes: <http://www.rmrs.nau.edu/mistletoe>  
> Stem Rusts: <http://www.rmrs.nau.edu/rust>



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